Hybridization between *Juniperus grandis, J. occidentalis* and *J. osteosperma* in northwest Nevada II: Terpenes, Buffalo Hills, Northwestern Nevada

Robert P. Adams
Biology Department, Baylor University, Box 97388, Waco, TX, 76798, USA
email Robert_Adams@baylor.edu

ABSTRACT

The volatile leaf oils of *J. grandis, J. occidentalis, J. osteosperma* and putative hybrids in northwestern Nevada along hwy 446 (Buffalo Hills) were analyzed. No evidence of hybridization involving *J. grandis* was found among the presumed hybrids and backcrosses of *J. occidentalis* and *J. osteosperma*. In fact, the terpene data was relatively uniform, suggesting that the complex concerned is a stabilized hybrid population. No plants having typical terpenes, of *J. occidentalis* and *J. osteosperma* were found. The terpene analysis seems in agreement with the haplotype data of Terry (2010).

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KEY WORDS: *J. grandis, J. occidentalis, J. osteosperma,* hybridization, Cupressaceae, terpenes, Buffalo Hills, northwestern Nevada.

Vasek (1966) published the seminal paper on hybridization among species of *Juniperus* in north-western Nevada. Based on exhaustive field work and morphological data, he concluded that *J. occidentalis* and *J. osteosperma* were hybridizing across a large area of northwestern Nevada. His careful observations and analyses were confirmed by Terry et al. (2000) and Terry (2010), who found cpDNA (trnL-trnF, trnS-trnG) haplotypes of *J. occidentalis* in Nevada populations of *J. osteosperma*, with lower frequencies occurring in Utah, Colorado, and Wyoming. Subsequently, Terry (2010) analyzed trnL-trnF and trnS-trnG (cpDNA) haplotypes and reported similar results (Fig. 1). He found that all samples of *J. occidentalis* from Oregon were uniform in having only haplotype 9 (Fig. 1). However, the NV 446 population had two of the *J. occidentalis* haplotypes and yet two other haplotypes (Fig. 1).

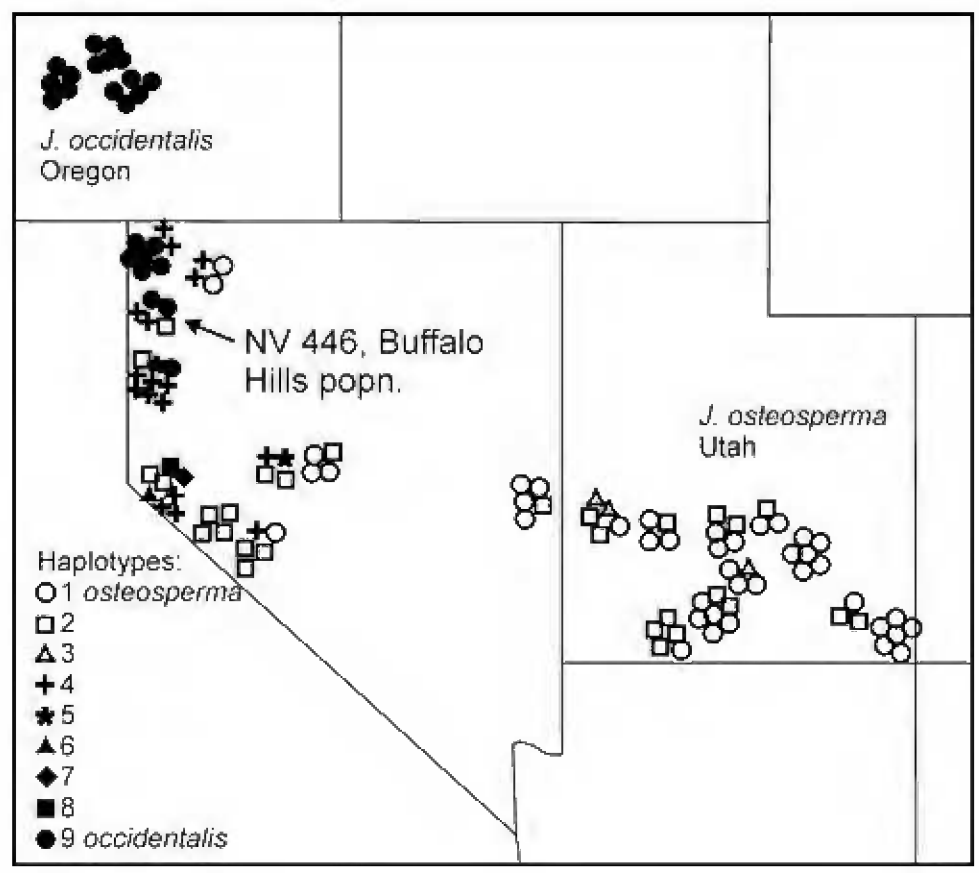

Figure 1. Distribution of haplotypes (trnL-trnF and trnS-trnG) in *J. occidentalis* and *J. osteosperma* (based on Terry, 2010).

J. grandis, *J. occidentalis, J. osteosperma* occupy generally allopatric ranges (Fig. 2), with *J. grandis* favoring granitic outcrops in the high Sierra, *J. occidentalis* growing on lava beds at lower elevations in northern California and Oregon, and *J. osteosperma*, preferring the intermediate elevations in the Basin and Range region of Nevada, Utah and adjacent states; a fourth species, *J. californica*, grows in the Mojave desert foothills of southern California, thence northward in the central valley foothills (Adams 2011). Adams (2012a, b) found that *Juniperus grandis* and *J. occidentals* appear to hybridize in the Beckwourth, CA area (Fig. 2) but, otherwise, no evidence of gene flow between these species was found (Adams and Kaufmann, 2010).

Juniperus grandis and *J. osteosperma* have been shown (Adams 2013) to hybridize at the Leviathan Mine area of western Nevada (Fig. 2). It is interesting to note that plants typical of both parents were found, along with quite intermediate individuals, and those appearing to be backcrossed to *J. osteosperma*, but not to *J. grandis* (Fig. 2).

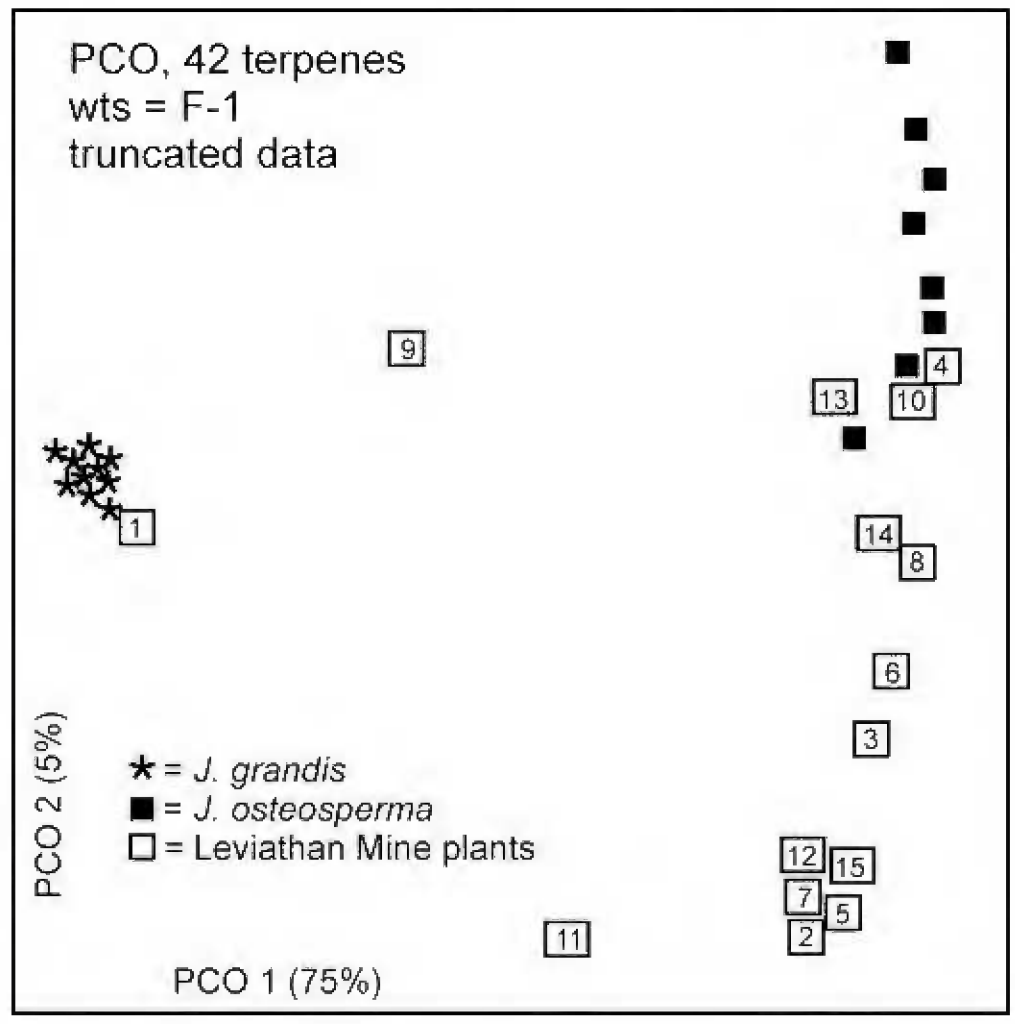

Figure 2. PCO of Juniperus from the Leviathan Mine with plants of the parental species (from Adams 2013).

The nw NV hwy 446 population, sampled by Terry (2010, popn. 18, Buffalo Hills) is in an area of sympatry between *J. occidentalis* and *J. osteosperma* (Fig. 3) and subject to ancestral as well as possible current hybridization. Analysis of the terpenes from plants of the NV hwy 446 (Buffalo Hills) population is the purpose of this paper.

MATERIALS AND METHODS

Plant material: ***J. grandis***, *Adams 11963-11967*, Jct. US 50 & CA 89, 38° 51.086' N, 120° 01.244' W, 1937 m, Meyers, El Dorado Co.; CA; *Adams 11968-11972*, 16 km w of Sonora Jct., on CA. 108, 38° 18.289' N, 111° 35.598' W, 2585 m, Tuolumne Co.; CA, ***J. osteosperma***, *Adams 1689-1699, 1701-1705,* on US 6, Thistle, 40° 00' 6.9" N, 111° 29' 4.6" W, 1650 m, Utah Co., UT, *Adams 12067-12071*, 4 km n of Sedona, AZ, at Grasshopper Point, on Alt US 89, 34.888° N, 111.733° W, 1380m, Coconino Co., AZ, *Adams 10272-10276,* on NV157, Charleston Mtns., 36° 16.246' N, 115° 32.604' W, 1795 m, Clark Co., *J.* NV; *Adams 11122-11124,* Hancock Summit, mile 38 *occidentalis (in part) and J. osteosperma* on US 375, 37° 26.404' N, 115° 22.703' W, 1675 m, (in part) with Leviathan mine population noted. Lincoln Co. NV; *Adams 11125-11127*, McKinney Tanks Summit on US 6, 38° 07.005' N, 116° 54.103' W, 1933 m, Nye Co., NV; *Adams 11134-36*, 8 km s of Bridgeport, on US395, 38° 12.639' N, 119° 13.846' W, 2004 m, Mono Co., CA; *Adams 11141-11143,* 13 km w of Elko, on I 80, 40° 45.598' N, 115° 55.942' W, 1535 m, Elko Co., NV; *Adams 11144-11146*, 8 km e of of Wells, on I 80, 41°06.533' N, 114°51.441' W, 1876 m, Elko Co., NV; *Adams 11960-11962,* 56 km

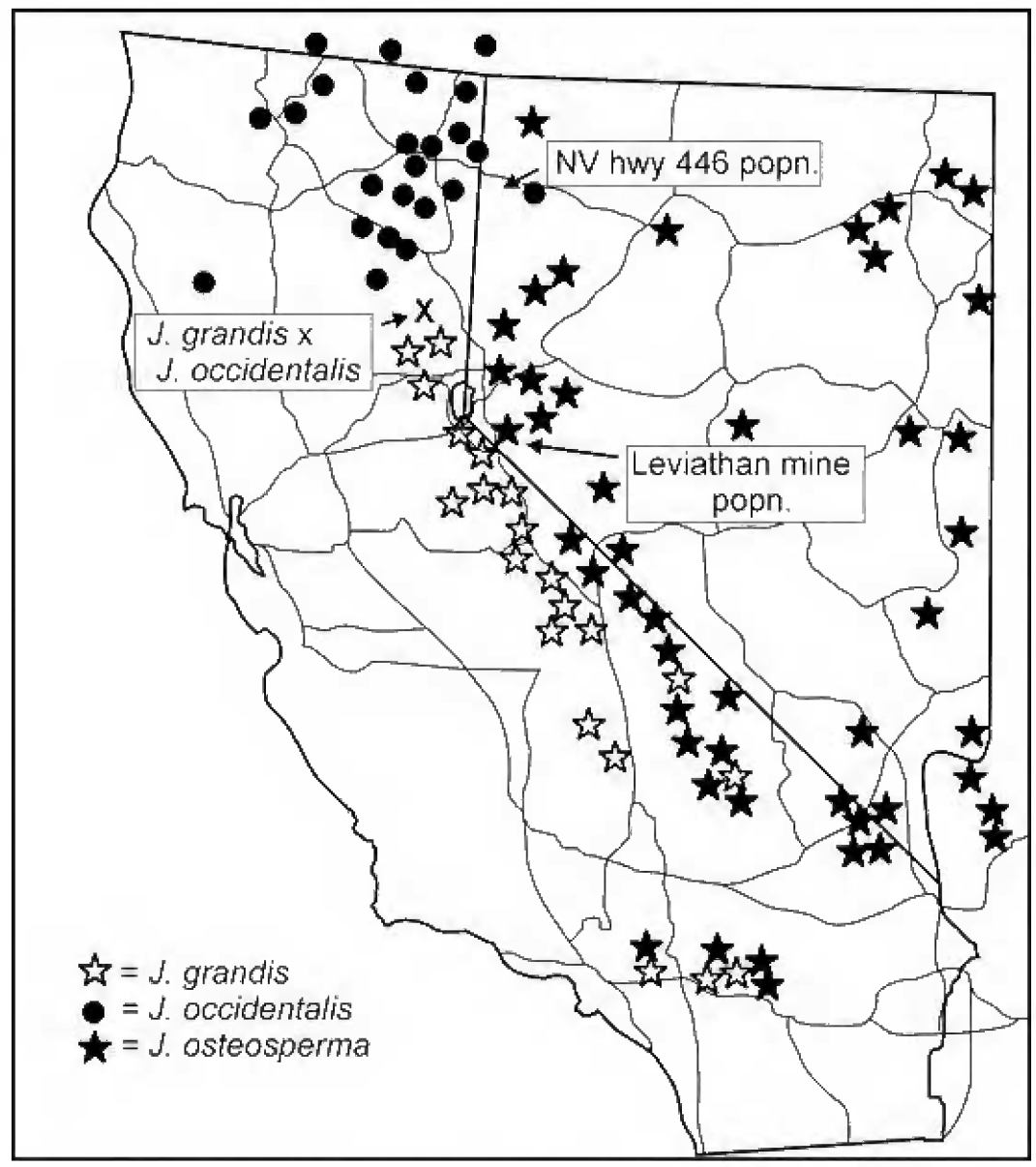

Figure 3. Distribution of three western junipers and the location of the NV hwy 446 population of this study. The eastern distribution of *J. osteosperma* is not shown.

n of Reno, NV; on US 395, 39° 54.458' N, 120° 00.322' W, 1383 m, Lassen Co., CA; *Adams 11973-11977,* 10 km n of CA 168 on White Mtn. Rd., 37° 20.143' N, 118° 11.346' W, 2607 m, Inyo Co., CA; *Adams 11978-11982,* Mahogany Flats Campground, Panamint Mtns., 36° 13.783' N, 117° 04.102' W, 2477 m, Inyo Co., CA, *Adams 12323-12327*, Basin, San Bernardino Mtns., 34° 16.910' N, 116° 45.306' W, 1820 m, San Bernardino Co., CA, *Adams 12210-12214*, ca. 1 km e of CA 18, ca. 16 km s of jct CA 18 & CA 247, n slope San Bernardino Mtns., 34° 21.213' N, 116° 50.607' W, 1393 m, San Bernardino Co., CA, *Adams 12215-12219*, on I15, at Bailey Rd., 35° 27.938' N, 115° 31.709' W, 1431 m, San Bernardino Co., CA. ***J. occidentalis***, *Adams 11940-11942,* 12 km e of Jct. WA 14 & US 97 on WA 14, 45° 44.392' N, 120° 41.207' W, 170 m, Klickitat Co.; WA, *Adams 11943-11945*, 2 km s of jct. US 97 & US 197 on US 97, 38 km ne of Madras, OR; 44° 53.676' N, 120° 56.131' W, 951 m, Wasco Co., OR; *Adams 11946-11948*, 3 km sw of Bend, OR; on OR 372, 44° 02.390' N, 121° 20.054' W, 1132 m, Deschutes Co., OR; *Adams 11949-11951,* 32 km e of Bend, OR on OR 20, shrubs, 0.5 - 1m tall, 43° 53.922' N, 120° 59.187' W, 1274 m, Deschutes Co., OR; *Adams 11952-11954,* 14 km e of Jct. OR66 & I 5, on OR66, 42° 08.044' N, 122° 34.130' W, 701 m, Jackson Co., OR; *Adams 11957-11959*, on CA 299, 10 km e of McArthur, CA, 41° 05.313' N, 121° 18.921' W, 1091 m, Lassen Co., CA; *Adams 11995-11998 (Kauffmann A1-A3, B1),* Yolla Bolly-Middle Eel Wilderness, 40° 06' 34" N, 122° 57' 59" W, 1815- 2000 m, Trinity Co., CA, *Adams 12342-12346*, 19 km WSE of Susanville, CA, on CA 36, 40° 22.178' N, 120° 50.211' W, 1570 m, Lassen Co., CA, *Adams 12347-12351*, on US 395, 5 km n of Madeline, 41° 05.867' N, 120° 28.456' W, 1695 m, Lassen Co., CA. **northwestern Nevada, hwy 446 population**: *Adams 12352-12366*, at mile 98, NV hwy 446 [=Terry (2010) popn.#18, Buffalo Hills], 40° 53.104' N; 119° 36.212' W, 5667 ft. Voucher specimens are deposited in the herbarium, Baylor University (BAYLU).

Isolation of Oils - Fresh leaves (200 g) were steam distilled for 2 h using a circulatory Clevenger-type apparatus (Adams, 1991). The oil samples were concentrated (ether trap removed) with nitrogen and the samples stored at -20°C until analyzed. The extracted leaves were oven dried (100°C, 48 h) for determination of oil yields.

Chemical Analyses - Oils from 10-15 trees of each taxon were analyzed and average values reported. The oils were analyzed on a HP5971 MSD mass spectrometer, scan time 1/ sec., directly coupled to a HP 5890 gas chromatograph, using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column (see Adams, 2007 for operating details). Identifications were made by library searches of our volatile oil library (Adams, 2007), using the HP Chemstation library search routines, coupled with retention time data of authentic reference compounds. Quantitation was by FID on an HP 5890 gas chromatograph using a J & W DB-5, 0.26 mm x 30 m, 0.25 micron coating thickness, fused silica capillary column using the HP Chemstation software. Terpenoids (as per cent total oil) were coded and compared among the species by the Gower metric (1971). Principal coordinate analysis was performed by factoring the associational matrix using the formulation of Gower (1966) and Veldman (1967). Principal components analysis (PCA) follows the formulation of Veldman (1967).

RESULTS AND DISCUSSION

To determine if *J. grandis* might be involved in hybridization in this population, ANOVA was performed on the leaf oil components of *J. grandis, J. occidentalis* and *J. osteosperma* (data from Adams 2013). The resulting F ratios (from ANOVA) were used as character weights (i.e., F-1.0) to produce a matrix of similarities that was factored by PCO and ordinated (Fig. 4). From this ordination, there does not appear to be any of the putative hybrids that are tending to cluster with *J. grandis*, lending credence that *J. grandis* is not genetically involved in the nw NV, hwy 446 population. Of course, ancient hybridization and introgression might have had a very subtle effect on the leaf oils, and such events can not be eliminated.

The leaf oil compositions of *J. occidentalis* and *J. osteosperma* have 19 highly significant, and 2 significant differences (Table 1). Interestingly, two of the largest components, sabinene (11.5 - 12.9%)

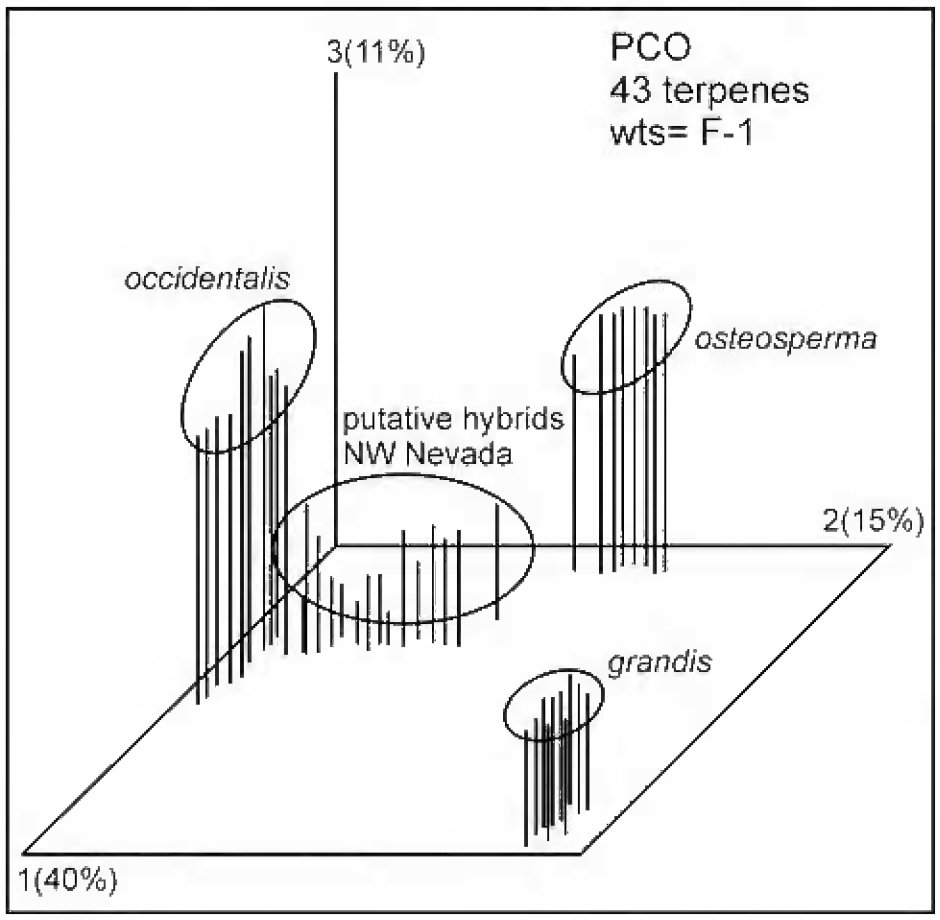

Figure 4. PCO of *J. grandis, J. occidentalis, J. osteosperma* and putative hybrids from NW NV.

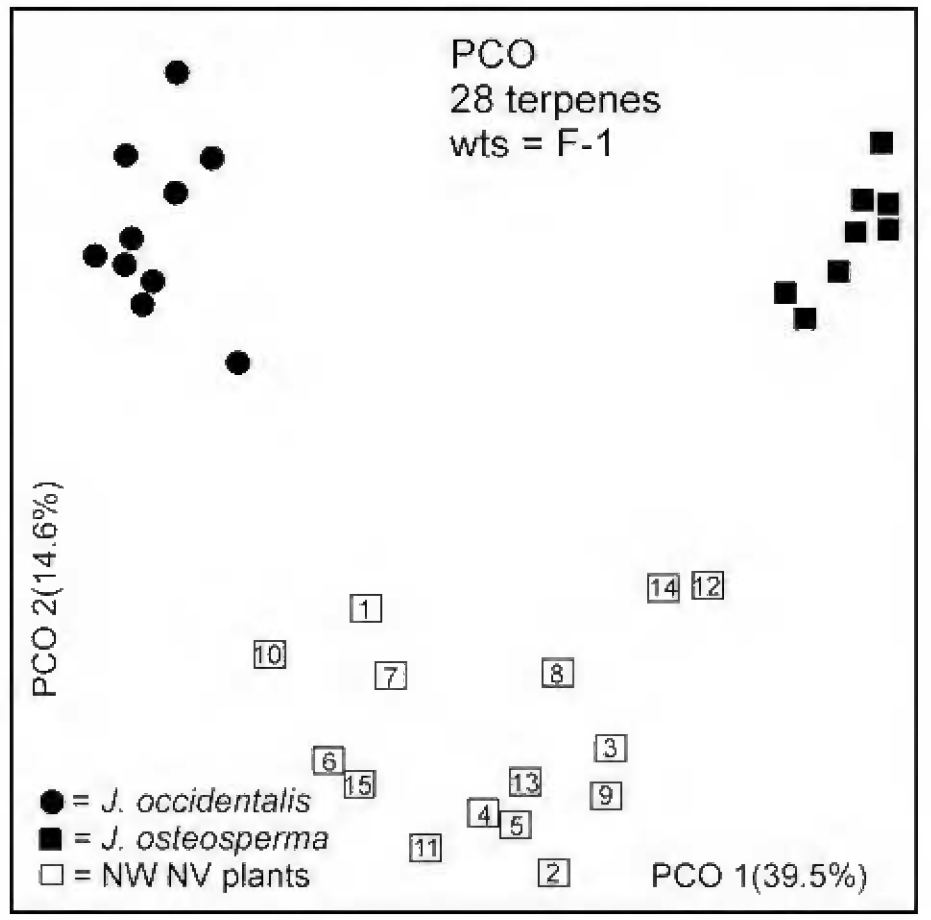

Figure 5. PCO of *J. occidentalis, J. osteosperma* and plant from NW NV. see text for discussion.

and bornyl acetate (13.3 - 13. 6%) were not significantly different. Sabinene is notable in being found in higher concentration in the putative hybrids than in the parents (14.9 - 30.5%). Twenty nine of the compounds were used to compute similarity measures using character weights of F-1.0 (F from ANOVA between the parents). Factoring the similarity matrix by PCO gave eigenroots that accounted for 39.5, 14.6, 5.8, 5.4 and 4.46% of the variance among plants. Ordinating the data on the first two axes shows *J. occidentalis, J. occidentalis,* and the plants from nw NV as a third group (Fig. 5). Within the NV plant group, individuals 12 and 14 (Fig. 5) appear to have oils intermediate to *J. osteosperma*; whereas plants 1, 7, and 10 show an affinity to *J. occidentalis*. It may be that these plants represent backcrossed individuals, or some linkage group as found in *Cryptomeria japonica* artificial hybrids (Adams and Tsumura, 2012), or this may be a case of dominant/ recessive terpenes influencing the similarities as reported in Douglas fir (Adams and Stoehr, 2013). However, in the case of Douglas fir synthetic hybrids, the dominant terpenes place a number of F_1 hybrids near one parent, not both parents as in the present case. So it seems more likely that plants 1, 10, 12, and 14 are backcrossed individuals.

It is interesting to compare the patterns in the Leviathan mine (Fig. 2) and the nw NV population (Fig. 5). The Leviathan mine area clearly contained both parents as their oils were typical of *J. grandis* and *J. osteosperma*. In contrast, in the nw NV population, no plants clustered with *J. occidentalis* or *J. osteosperma*. Of course, as the purpose of this study was to document hybridization, it is likely that the author collected from those plants showing intermediate morphology. Table 2 shows field notes on the 15 trees sampled and the subsequent terpene assessment of their identities. Several of the plants field identified as *J. osteosperma* (2, 4, 7) had hybrid terpene patterns (Fig. 5). Plant 8, field-identified as *J. occidentalis*, was found to be quite intermediate in its terpenes (Fig. 5) and another plant identified as *J. occidentalis* ? (#10), appears to be a backcross to *J. occidentalis*; in short, these two species are difficult to identify in nw NV, and it is likely that specimens have been misidentified in the past.

Table 1. Morphological observations on plants of the NV 446 (Buffalo Hills) population.
bc occ = backcross to *J. occidentalis*, bc ost = backcross to *J. osteosperma*.

occid x osteo, Washoe Co, NV

coll#(id #)	morph, in field	terpenes, this study	monecious?	# stems	glands visible	ruptured glands
occid	occid	occid	50% monec	1(-3)	visible	ruptured
osteo	osteo	osteo	90% monec	several	not conspicuous	not-ruptured
12352 (1)	bc occ	bc occ	monec.	1 stems	not visible	few ruptured
12353 (2)	osteo	hybrid	female	8 stems	not visible	v. few ruptured
12354 (3)	hybrid	hybrid	monec	5 stems	visible	not ruptured
12355 (4)	osteo	hybrid	female	3 stems	not visible	not ruptured
12356 (5)	occid	hybrid	female	1 stems	visible	ruptured
12357 (6)	hybrid	bc occ	female	10 stems	visible	ruptured
12358 (7)	osteo	bc occ	male	10 stems	not visible	not ruptured
12359 (8)	occid	hybrid	monec	1 stems	visible	ruptured
12360 (9)	hybrid	hybrid	monec	3 stems	visible	ruptured
12361 (10)	occid?	bc occ	female	1 stems	not visible	not ruptured
12362 (11)	hybrid	hybrid	monec	5 stems	visible	ruptured
12363 (12)	hybrid	bc ost	monec	4 stems	visible	ruptured
12364 (13)	hybrid	hybrid	female	1 stems	visible	ruptured, white exud
12365 (14)	hybrid	bc ost	female	5 stems	visible	ruptured, white exud
12366 (15)	hybrid	bc occ	monec	6 stems	visible	ruptured, white exud

CONCLUSIONS

The nw NV population along hwy 446 (Buffalo Hills of Terry, 2010) appears to be composed of chiefly hybrids and possible backcrosses, in contrast to the Leviathan Mine population that contains both parents, hybrids and backcrosses to only *J. osteosperma*. The uniformity of the nw NV population seems unusual for a hybrid swarm, and suggests that it may be a stabilized hybrid population. Additional research will be needed to elucidate this unusual pattern.

ACKNOWLEDGEMENTS

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Table 2. Leaf essential oil compositions for *J. occidentalis* and *J. osteosperma* plus #2, 5 (putative hybrids), #10 (putative backcross to *J. occidentalis*) and #12 (putative backcross to *J. osteosperma,* (see Fig. 4). Compounds in boldface were used in PCO analysis. F from ANOVA between *J. occidentalis* and *J. osteosperma.* significance: * = 0.05; ** = 0.01; ns = not significant, nt = not tested in ANOVA.

KI	compound	occid	osteo	#2	#5	#10	#12	F ex ANOVA
921	**tricyclene**	**0.8**	**0.5**	**0.4**	**0.4**	**0.3**	**0.6**	**2.5 ns**
924	**α-thujene**	**1.2**	**0.6**	**0.6**	**0.7**	**0.9**	**0.5**	**23.1 ****
932	**α-pinene**	**3.6**	**4.2**	**2.9**	**2.4**	**2.7**	**3.6**	**1.2 ns**
945	α-fenchene	t	-	-	t	t	0.2	nt
946	**camphene**	**0.8**	**0.7**	**0.4**	**0.5**	**0.4**	**0.7**	**1.2 ns**
953	thuja-2,4-diene	t	t	-	-	-	-	nt
961	verbenene	0.9	t	-	t	-	-	nt
969	sabinene	12.9	11.5	22.1	23.0	30.5	14.9	ns
974	β-pinene	0.4	0.2	0.5	0.1	0.1	0.4	ns
988	**myrcene**	**1.9**	**1.4**	**2.5**	**2.0**	**2.6**	**2.6**	**2.8 ns**
1001	δ-2-carene	t	-	-	-	-	-	nt
1002	**α-phellandrene**	**0.8**	**0.3**	**0.2**	**0.1**	**0.2**	**0.1**	**23.3 ****
1008	**δ-3-carene**	**1.6**	**-**	-	**0.3**	-	**5.4**	**7.4 ****
1014	**α-terpinene**	**1.9**	**1.6**	**2.5**	**1.8**	**2.8**	**1.4**	**2.2 ns**
1020	**p-cymene**	**10.4**	**2.4**	**0.5**	**0.6**	**0.6**	**0.4**	**23.5 ****
1024	**limonene/β-phellandrene**	**1.2**	**2.2**	**5.1**	**3.7**	**3.5**	**5.6**	**23.4 ****
1044	(E)-β-ocimene	0.1	t	0.7	0.4	0.4	0.8	ns
1054	**γ-terpinene**	**3.2**	**2.5**	**4.2**	**3.0**	**4.5**	**2.3**	**3.2 ns**
1065	**cis-sabinene hydrate**	**0.8**	**1.1**	**1.9**	**1.7**	**1.4**	**1.2**	**5.2 ns**
1086	**terpinolene**	**1.5**	**1.3**	**1.7**	**1.2**	**1.1**	**1.9**	**2.9 ns**
1095	linalool	0.5	-	t	t	t	0.1	nt
1098	**trans-sabinene hydrate**	**0.6**	**1.4**	**1.5**	**1.1**	**1.1**	**1.0**	**227.5 ****
1118	cis-p-menth-2-en-1-ol	0.7	0.6	0.9	0.6	0.8	0.6	ns
1136	**trans-p-menth-2-en-1-ol**	**0.8**	**-**	**0.5**	**0.2**	**0.5**	**-**	**227.6 ****
1141	**camphor**	**1.4**	**21.3**	**4.9**	**6.9**	**0.8**	**21.7**	**108.6 ****
1145	**camphene hydrate**	**0.2**	**1.4**	**1.2**	**1.0**	**0.4**	**1.2**	**336.5 ****
1154	**sabina ketone**	**0.4**	**1.1**	**0.1**	**0.2**	**0.1**	**0.3**	**68.4 ****
1165	**borneol**	**1.1**	**4.8**	**0.5**	**0.5**	**0.1**	**1.5**	**22.3 ****
1166	**coahuilensol**	**1.2**	**t**	t	**3.3**	**0.2**	**0.4**	**35.6 ****
1174	**terpinen-4-ol**	**7.6**	**9.8**	**12.0**	**8.4**	**12.0**	**6.7**	**5.2 ***
1179	p-cymen-8-ol	0.5	0.5	t	-	t	0.2	nt
1186	α-terpineol	0.4	0.4	0.7	0.5	0.6	0.5	ns
1195	myrtenol	-	0.2	t	t	t	t	nt
1195	cis-piperitol	0.2	0.3	0.3	0.3	0.2	0.1	nt
1204	verbenone	-	0.2	-	-	-	-	nt
1207	trans-piperitol	0.3	0.3	0.5	0.3	0.3	0.4	nt
1215	trans-carveol	-	0.6	-	-	-	-	nt
1219	coahuilensol, me-ether	1.1	0.2	t	6.8	0.5	0.4	ns
1230	trans-chrysanthenyl ac.	-	-	0.8	-	-	-	nt
1238	cumin aldehyde	0.2	0.3	-	-	-	-	nt
1239	carvone	-	0.6	-	-	-	-	nt
1249	piperitone	0.2	t	t	-	-	-	nt
1257	methyl citronellate	-	-	0.3	-	t	-	nt
1283	α-terpinen-7-al	-	0.2	-	-	-	-	nt
1284	bornyl acetate	13.6	13.3	14.8	15.5	10.3	13.7	0.01 ns
1298	carvacrol	0.4	t	0.2	0.3	0.2	0.4	nt
1318	**149,69,91,164, phenolic**	**-**	**0.4**	**0.8**	**0.4**	**2.9**	**2.6**	**33.8 ****
1318	methyl geranate	1.6	-	-	-	-	-	nt
1325	p-mentha-1,4-dien-7-ol	t	0.5	-	-	-	-	nt
1387	β-bourbonene	0.2	-	-	-	-	-	nt

KI	compound	occid	osteo	#2	#5	#10	#12	F ex ANOVA
1429	cis-thujopsene	0.9	0.7	-	-	-	-	nt
1451	trans-muurola-3,5-diene	0.1	-	-	-	-	-	nt
1465	cis-muurola-4,5-diene	0.1	-	-	-	-	-	nt
1468	**pinchotene acetate**	**1.0**	**0.1**	**t**	**2.2**	-	-	**7.2** *
1475	trans-cadina-1(6),4-diene	0.3	-	-	-	-	-	nt
1478	γ-muurolene	0.8	-	-	-	-	-	nt
1484	germacrene D	0.3	-	-	-	-	-	nt
1493	trans-murrola-4(14),5-diene	0.4	-	-	-	-	-	nt
1493	epi-cubebol	0.4	-	-	-	-	-	nt
1500	α-muurolene	1.1	t	t	t	t	-	nt
1513	**γ-cadinene**	**1.9**	**t**	**0.5**	**0.3**	**0.7**	**0.1**	**34.3** **
1518	epi-cubebol	0.4	-	-	-	-	-	nt
1522	**δ-cadinene**	**2.4**	**0.5**	**0.8**	**0.8**	**0.7**	**0.4**	**15.2** **
1537	α-cadinene	0.4	-	-	-	-	-	nt
1544	α-calacorene	0.3	-	-	-	-	-	nt
1548	**elemol**	**0.2**	**1.3**	**0.7**	**0.3**	**6.2**	**0.6**	**52.3** **
1574	**germacrene-D-4-ol**	**0.5**	**0.1**	**1.0**	**0.7**	**0.4**	**0.4**	**21.3** **
1582	caryophyllene oxide	-	t	-	-	-	-	nt
1586	gleenol	0.3	-	-	-	-	-	nt
1607	β-oplopenone	0.3	t	0.7	0.3	0.2	0.2	nt
1608	humulene epoxide II	-	t	-	-	-	-	nt
1618	1,10-di-epi-cubenol	0.2	-	-	-	-	-	nt
1627	1-epi-cubenol	1.6	-	t	0.4	0.5	-	nt
1630	γ-eudesmol	-	0.2	-	-	0.6	-	nt
1638	**epi-α-cadinol/muurolol**	**0.7**	**t**	**1.5**	**0.8**	**1.2**	**0.6**	**55.1** **
1644	α-muurolol	0.2	-	0.1	0.1	0.2	t	nt
1649	β-eudesmol	-	0.2	0.1	t	0.7	t	nt
1652	α-eudesmol	-	0.2	t	-	1.2	-	nt
1652	**α-cadinol**	**1.3**	**0.3**	**2.4**	**1.1**	**1.3**	**1.0**	**43.7** **
1739	oplopanone	-	t	0.2	t	t	t	nt
1870	198, 205, 220, 149	-	-	0.3	0.5	0.4	0.4	nt
1987	manoyl oxide	2.2	-	t	t	t	0.1	nt
2009	epi-13-manoyl oxide	t	-	-	-	-	-	nt
2312	abieta-7,13-dieen-3-one	-	0.1	-	-	-	t	nt

KI = linear Kovats Index on DB-5 column. Compositional values less than 0.1% are denoted as traces (t). Unidentified components less than 0.5% are not reported.